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BOTANICAL GAZETTE

AUGUST, 1906

THE NASCENT FOREST OF THE MISCOU BEACH PLAIN.

CONTRIBUTIONS TO THE ECOLOGICAL PLANT GEOGRAPHY OF THE PROVINCE OF NEW BRUNSWICK, NO. 4.[1]

W. F. GANONG.

(WITH FOURTEEN FIGURES)

THE extreme northeastern angle of the Province of New Brunswick, as the accompanying map will show, is formed by the island of Miscou. The northwestern margin of this island is an extensive sandy beach plain, growing rapidly by action of the sea, locally called Grande Plaine. On this plain there is developing a forest which exhibits every stage of formation from the salt plants of the open sea beach to the heterogeneous vegetation of the mixed woods. The conditions are unusual and the phenomena of proportional interest. In August 1905 I was able to give the place some two weeks of observational study, with results which follow.

In all such studies as this the correct identification of the plants is of first importance, and identification is becoming a matter of such difficulty that only a professional systematist is competent authority. Accordingly I have sent all of my collections, including a specimen of every plant I found at Grande Plaine, to Professor M. L. FERNALD, of the Gray Herbarium of Harvard University, who has been so kind as to determine their identity, and, as well, to give me the names they should bear in accordance with the recommendations of the Vienna Congress. I wish here to express my indebtedness to him and my best thanks for this invaluable aid. Such is the origin of the nomenclature of this paper.

[1] No. 3 is in the BOT. GAZETTE **36**:161–186, 280–302, 349–367, 429–455. 1903.

As to previous literature of this particular subject, there is none. In 1886 Dr. G. U. HAY made a collection of Miscou plants for the Geological Survey of Canada, but no account of them was ever published, and no other botanist has heretofore been on the island. In many respects, however, as the reader will observe, the vegetation of this beach plain resembles closely the vegetation

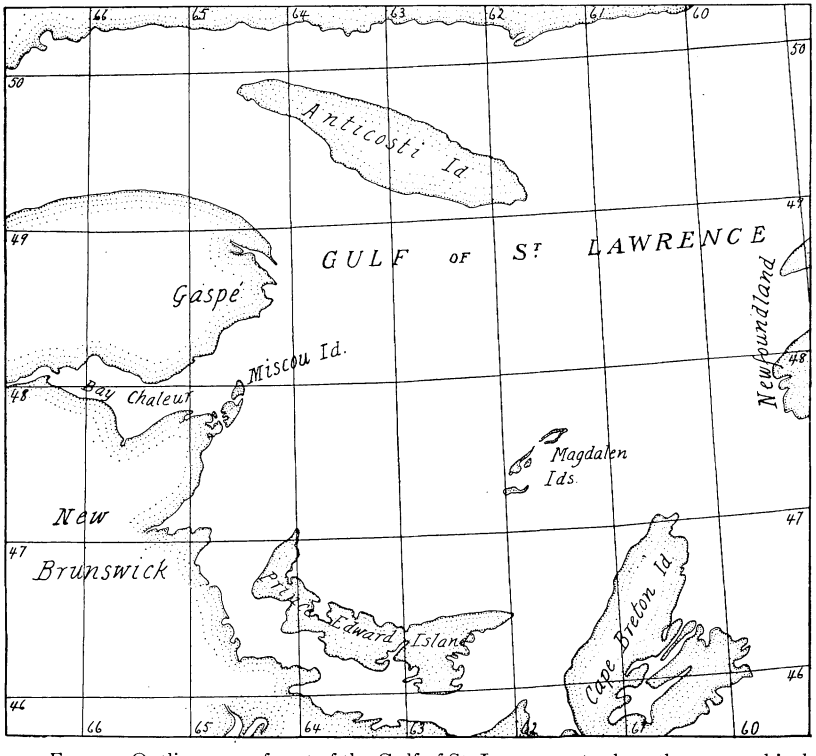

FIG. 1.—Outline map of part of the Gulf of St. Lawrence, to show the geographical position of Miscou Island.

of the sand beaches and dunes of Lake Michigan as described in COWLES'S well-known memoir,[2] and many of the conclusions of that work are also applicable here.

Grande Plaine extends along the west side of Miscou. Beginning on the south at Eel Brook (see the accompanying map, *fig. 2*),

[2] BOT. GAZETTE **27**:95–117, 167–202, 281–308, 361–391. 1899.

where it is but a few yards wide, it rapidly broadens northward until it reaches some half a mile across, and then narrows again towards its northern end, which is also the northernmost point of the island. Though nearly level as a whole, it is by no means flat, for it is composed of a series of approximately concentric dune beaches, which, two or three in number at Eel Brook, increase to over forty opposite Lac Frye. In height these dune beaches vary from two to five or six or even seven feet (0.6–2^{m}) and in breadth from eight or ten up to forty or fifty paces. At its widest part, which comprises some thirty or more of the beaches, new ones are plainly being rapidly added, while at its northern end the entire plain is being washed away by the sea, which is cutting sharply across the ends of the old beaches. About two-fifths of the plain, including the older parts next the upland, are forested; about two-fifths, including all the outer and newer parts, are open, clothed only by the waving beach grass; the intermediate zone, a small one-fifth of the area of the plain, is a

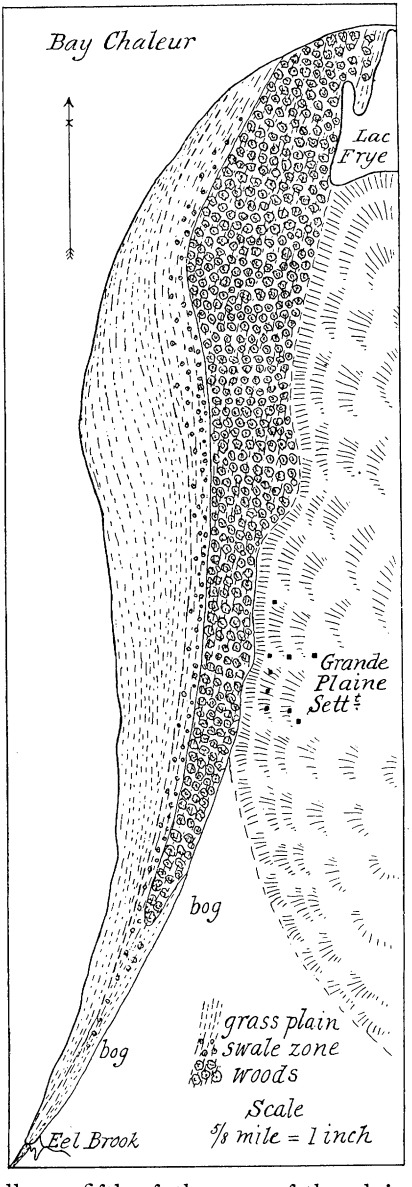

FIG. 2.—Map of Grande Plaine, Miscou Island; from an amateur survey by the author; dotted boundaries are only approximate; the heavier dotted line outside the swales represents approximately a line of higher dune beaches.

transition zone where the forest is pushing its advance into the open ground. The mode of formation of this remarkable plain, involving the anomaly of extensive land-building on a sinking coast, I have described somewhat fully elsewhere.[3] Briefly, the facts are these. As the result of peculiarities of the topography, wind, and tides of this region, there is formed on the shallow northwestern side of Miscou a kind of great eddy in which all movable materials, sand and gravel from the wear of the rapidly crumbling adjacent coasts, as well as driftwood, waterweeds, and other flotsam, often from a great distance, tend to collect, and thence are driven ashore by the prevailing westerly winds. Formerly the island extended farther north than now, carrying with it both eddy and plain; but the general subsidence actively in progress in this region has carried its low northerly end beneath the sea, thus forcing the eddy and the accompanying plain-building gradually southward. The northern end of Grande Plaine today is being rapidly washed away (compare map), to be redeposited farther south, and the plain as a whole is thus rolling by its outer margin southward along the coast. The subsidence of the land has produced another effect upon the plain, and one of considerable consequence to its vegetation, namely, its inner and older part averages somewhat lower, that is, less above sea-level, than the outer and newer part, thus leading to a settling of water towards the older inner parts, and a relatively higher water-table in them. That we have here a beach plain, instead of a series of lofty sand dunes, is the result of the fact, apparently, that the dry sand of the beach is blown ashore no faster than the beach grass can fix it. At both the northern and southern ends of the plain, however, there is some approach to a building of true, though low, dunes.

My brief study of the vegetation of Grande Plaine was entirely observational, not at all instrumental, nor do any meteorological or other exact physical data for this region exist. Grande Plaine lies at sea-level in latitude 48°, beside a shallow sea, warm in summer but frozen over in winter. The summer climate is remarkably equable, of a temperature most comfortable for man, with no fogs and but little cloudy weather. The rainfall must be not far from

[3] Bull. Nat. Hist. Soc. N. B. No. 24:453. 1906.

45 inches. Heavy winds from the west prevail in summer. The soil is of pure quartz sand derived from the wear of the gray carboniferous sandstones of the region, this sand having, of course, the usual relations to water-supply, mineral nutrients, etc. No other special factors with a bearing upon the vegetation appear to be prominent.

We turn now to consider the vegetation. Although it presents every gradation from humble herbs of the open beach to the densest woods, nevertheless the eye becomes accustomed to recognize, and the speech to designate, certain definite vegetational regions. These represent the modes or climaxes, as it were, in the vegetation curve —the parts which exhibit a distinctive character in the physiognomy of the whole. They are the following: (1) the new beach, (2) the grass plain, (3) the swales, (4) the sandy woods, (5) the closed woods.

THE NEW BEACH.

The characteristic open, or new, beach of Grande Plaine, the kind which best illustrates the mode of growth of the plain, is to be found opposite its middle and broadest part; for towards the northern and southern ends its structure is modified by local conditions of erosion and dune-building. Outside of all is a broad sloping inter-tidal beach of pure sand without vegetation (*fig. 3*). Above it is the narrow band between ordinary and extreme high tides, from which the drying sand is being driven landward by the winds; it is also vegetationless, or with but stragglers from the upper beach. Finally, there is that broad shelf, very well shown in the accompanying photograph (*fig. 4*), reached only by the very highest tides, composed of fine quartz sand, intermixed with some gravel and occasional flat cobbles; it is covered with scattered driftwood among and over which the dry sand is being forever driven, shifted, and piled. Thus the new beach offers a barren habitat to plants, for it has a mineral-poor soil, drenched often by salt, forever shifting, and exposed to the unbroken force of frequent heavy winds. The vegetation is plainly responsive to these conditions. It is extremely scanty, the plants growing widely isolated, while many square yards do not show any vegetation at all. Thus competition among the plants seems not to exist, and the struggle is wholly with the

physical environment. The most characteristic plant by far is the small, radiate-decumbent, succulent, annual saltwort, *Salsola*

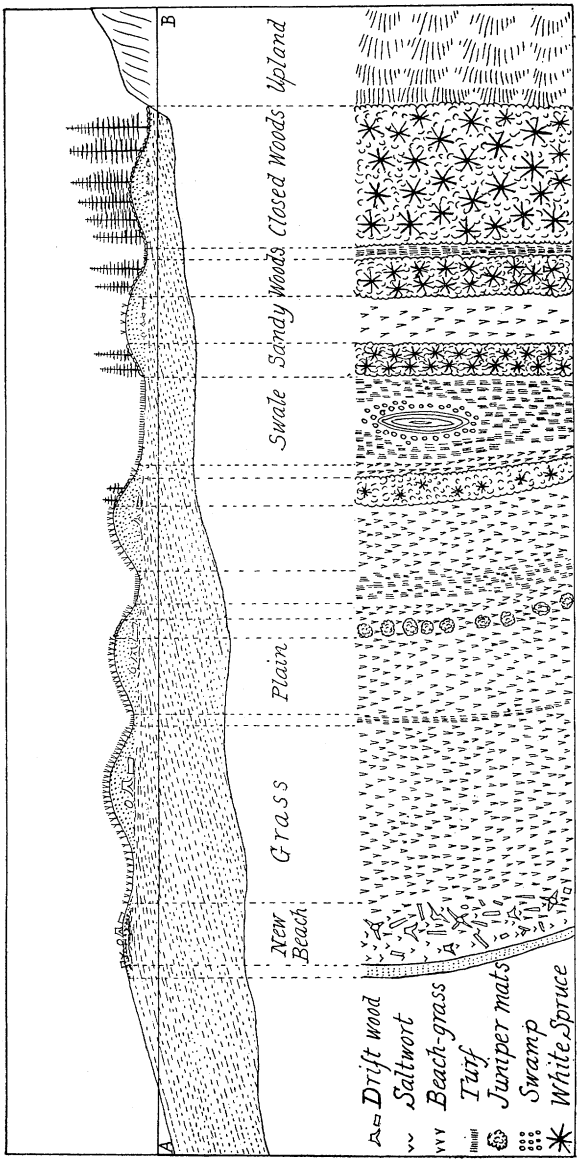

FIG. 3.—Idealized section and map to show the mode of formation of the beach plain, and the distribution of its vegetation; the line *AB* is true level, and may be taken to represent approximately the position of the water-table.

Kali, which occurs but rarely and for the most part in the lee of

some shelter, such as a hollow or large piece of driftwood. Next in abundance, though but scarce, is the little fleshy, rosette-like, annual sea rocket, *Cakile edentula* (*C. americana*). Third in abundance is the low halo-rosette, perennial sea lungwort, *Mertensia maritima*, here seemingly growing as an annual, also mostly in places of some shelter. Rarely, and then only in a sheltered position, occur tiny radiate-creeping plants of the beach pea, *Lathyrus maritimus*, growing apparently only as an annual, and sometimes showing a marked difference in the windward-creeping and leeward-

FIG. 4.—Typical open, or new, beach, looking north; among the driftwood occur scattered tufts of saltwort and beach grass.

creeping shoots on the same plant, the former being much shorter and smaller-leaved. Even rarer is the radiate-creeping, small-leaved, halo-scurfy annual, *Atriplex patula hastata*. Here and there, however, especially in sheltered places, arise the tufted culms of the beach grass, *Ammophila arenaria*, the characteristic sand-binding perennial of the dune beaches next to be considered, here seemingly growing from seed. I was able to find no other plants on the new beach. Thus we see that this vegetation is distinctly adjusted to the physical conditions, for it is of great paucity, of small and slow growth, annually renewed, closely ground-appressed, and strongly xerophytic.

THE GRASS PLAIN.

Inside the line of open beach begins the sand plain, composed of a great number of approximately parallel dune beaches, forming smoothly swelling ridges and hollows of elevations and breadths already described. Every dune beach, I believe, originates with a core of driftwood. As the tidal beach is built outwards by the addition of sand, driftwood continues to collect on its uppermost part, until finally some unusual combination of great winds with high tides sweeps it up beyond reach of further disturbance. Then the driving sand from the beach is caught among it; the beach grass gains a foothold in the sheltered places, spreads, and checks the further movement of this sand. Then more sand is driven shoreward, and it grows into a low dune which is fixed by the beach grass as fast as it rises. The limit is reached only when a new line of driftwood has been formed outside and begins to stop the sand for its own growth. The resultant dune beach offers severe conditions for plant life, for its surface is swept, especially on the summit and windward slope, by heavy winds; it is heated intensely by the sun; it is readily movable; and it forms a soil extremely poor in mineral nutrients.[4] It lacks the salt of the newer beaches, however, for this is soon removed by the rain; and it possesses an ample supply of moisture a foot or two beneath the surface, for the supply brought by the rain drains but slowly away, owing to the low gradient of the water-table. These conditions, especially at their extreme on the summits and windward slopes of the beach dunes, are endured by practically but a single plant—the herbaceous-perennial, subterranean-creeping, xero-culmed, deep-rooting beach grass, *Ammophila arenaria*, which occurs, without any competitor whatever, in open scattered tussocks, only partially covering the ground, as well shown in *fig. 5*, and in closer view in *figs. 6* and *7*. It happens that this grass is of considerable economic value to the neighboring farmers, who cut it and haul it for hay, and whose cattle graze upon it; its destruction in this way causes an irregular exposure of the outer beaches, permitting them to be irregularly cut by the wind. It is for this reason, I have no doubt, the newer outer beaches

[4] As indicated by KEARNEY'S recent studies: BOT. GAZETTE 37:426–436. 1904.

are so much more irregular in their various characters than the older inner beaches, which antedate the advent of man.

But while the beach grass has no competitor, it affords a shelter, especially behind its tussocks, permitting the growth of a number of other plants, which, however, form but an insignificant part of the entire vegetation, and which are widely separated from one another. Most important of these, perhaps, is the beach sedge *Carex silicea*, which grows in scattered tussocks here and there among the beach grass, and it is indeed the only other plant which

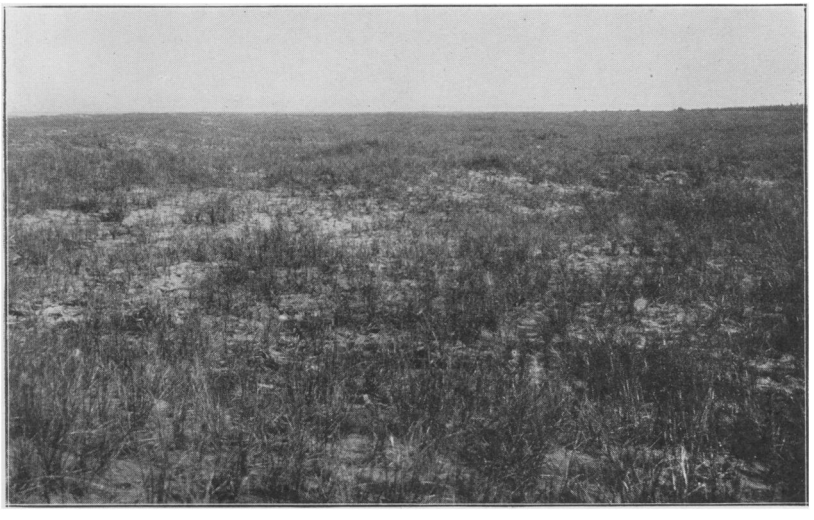

FIG. 5.—Typical grass plain, looking north; practically no plant visible except the beach grass.

seems at home in this situation. The remainder of the plants, all sparsely or rarely represented, are obviously stragglers from the most diverse habitats, many of them quite unexpected residents in such a situation. Thus, dwarfed saltwort strays in from the beach, and the beach pea is here somewhat more flourishing than on the open beach. Then there are greatly dwarfed individuals of certain ubiquitous forms able to endure a wide range of physical conditions, such as the dandelion, *Taraxacum officinale*, which extends in sheltered spots even to the outer margin of the plain; the Canada thistle, *Cnicus arvensis;* the sow thistle, *Sonchus arvensis;* the

field sorrel, *Rumex Acetosella*, in dwarfed-rosette, very red forms; the evening primrose, *Oenothera biennis;* and the moonwort, *Botrychium ternatum intermedium*. There are also some forms usually characteristic of rather a dry habitat, such as the pearly everlasting, *Anaphalis margaritacea*, and a western yarrow, *Achillea lanulosa*. In addition there are others, generally in more sheltered spots and also greatly dwarfed, which usually prefer a moister habitat, such as the two western roses, *Rosa acicularis* (*R. Sayi*, *R. Engelmanni*) and *Rosa lucida;* a western violet, *Viola adunca;* a stitchwort, *Stellaria longipes laeta;* a silver weed, *Potentilla Anserina concolor;* the stellate false Solomon's seal, *Smilacina stellata;* and one of the vetches, *Vicia Cracca*.[5] The great diversity of natural habit of these plants, their scanty and irregular occurrence, and their dwarfed size and rosette-forming tendency all unite to show that none of them are here at home. Obviously they are the ones which, of all the many kinds which must be brought to this plain by natural modes of dissemination, are sufficiently tolerant physiologically to be able to germinate under, and then to withstand, these extreme physical conditions, eking out here a starved and precarious existence. The conditions for germination upon the sand must be extremely severe, and it is very likely that other kinds of plants could exist here as adults, could their seeds develop; and further it is probable that the individuals which do exist on the plain are those whose seeds happened to fall in especially favorable spots, or became properly buried by the moving sand. Else why are they so few? The universal dwarfing is due in all likelihood not to the heat and dryness of the surface, nor to any salt content in the soil, and certainly not to a scarcity of soil water, but to the paucity of mineral nutrients in the sand. This is in harmony with another feature they mostly show in common—very deep and, I think, much-branching roots. The fact that they come

[5] The following Grande Plaine plants appear to be new to the flora of New Brunswick: *Achillea lanulosa*, *Viola adunca*, *Rosa acicularis*, *Stellaria longipes laeta*, and *Potentilla Anserina concolor*. Certain others are new in name, the species having been recently more exactly defined and segregated: *Alnus mollis*, *Myrica carolinensis*, *Vaccinium Vitis-Idaea minor*. Others are new in name because made to conform to the rules of the Vienna Congress, but in these cases the names of Gray's *Manual*, 6th edition, have been given in brackets.

from such a diversity of natural habitats, and yet live in this peculiar situation upon an equal footing, shows how far we are from understanding the real bases of physiological adaptation, and further shows that in the study of the physiological life-histories of plants lies the most important and attractive field for the ecologist of the near future.

So much for the exposed parts of the dune beaches. But in addition they offer, upon their inner or leeward slopes and in the hollows, situations more sheltered, not so much from the sun, since

FIG. 6.—Typical hollow between outer dune beaches; the tall grass is all beach grass, but the small plants among it are the common strawberry.

their average course is nearly north and south, but from the westerly winds. The older inner dune beaches also are protected to some extent by the newer outer ones, as well as by their slightly lower average level. The difference between leeward slope and hollow is not simply one of degree of shelter, however, but also of physical conditions, for the hollow is much nearer the source of water supply, the free table of which is not over a foot or two beneath the surface. In consequence of these differences we can recognize three distinct phases of vegetation: *first*, a larger development on the leeward

slopes of plants which are small and rare on the outer slopes; *second*, a distinctive vegetation of the hollows; and, *third*, a distinctive vegetation of the inner slopes.

As to the first phase, it is enough to note that several plants, in particular the pearly everlasting and the wild roses, small, scarce, and scattered on the outer slopes, become larger, frequent, and even patch-forming on the inner; and this is true also in less degree of other species. The beach grass persists in all situations.

The second phase is the vegetation of the hollows. The very first plant to appear in this situation, and that too near the outer beaches, is always, strangely enough, the common wild strawberry, *Fragaria virginiana*, apparently of normal size and form, seemingly quite at home, and spreading abundantly by runners, so that it forms considerable patches. The appearance of the nascent patches is well shown in *fig. 6*. As soon as the patches reach an appreciable density, such that they afford a cover to the ground, then turf-forming grasses, of which the first is the red fescue, *Festuca rubra*, appear and initiate the turf-formation which is so important a feature of the swales to be described below. The strawberry, of course, is one of the most tolerant, and hence ubiquitous, herbs of our flora, and its situation here is partially explained by the nearness of the abundant water supply. Yet it is surprising to find it taking so important a part in a vegetation in so peculiar a position.

The third phase of this vegetation is that characteristic of the sheltered slopes. First of such plants to appear, and the most common and characteristic, is the dwarf creeping juniper, *Juniperus Sabina procumbens*, of which single plants originate just below the beach dune crests, and creep radiating, more to leeward than to windward, in a close dense mat covering many square feet. A young plant is shown in *fig. 7*, in characteristic form and position. On the inner beaches these plants occur upon the outer as well as the inner slopes, and the shelter of the mats thus formed affords in reality the principal starting-point for the development of other plants which lead gradually to the development of the forest, as will be noted under the transition vegetation. In a similar situation, but independently, arise patches of two other characteristic plants, a bright-green, leathery-leaved, tufted shrub, the wax berry,

Myrica carolinensis, which comes to form dense discoid (sometimes almost fairy-ring like) masses on the crests and inner slopes; and the less frequent, low, dense-tufted, white-hairy shrub, *Hudsonia tomentosa*, in irregular close patches. All of these plants are pronounced xerophytes, which amply explains their ability to live in this situation, and even their preference for the somewhat drier upper slopes of the dune beaches. Their xerophilism, in common with that of many other evergreen sand plants, is, as I guess it, an

FIG. 7.—Typical upper inner slope of a dune beach; the grass is beach grass, but in the center is a typical plant of dwarf creeping juniper.

adaptation to the physiological dryness which results when, as must often be the case in spring and fall, the ground water is of low temperature and hence slowly absorbed, while the leaves are exposed to high transpiration conditions from the bright sun, heat reflected from the sand, and high winds.[6] The juniper, while perfectly at home here, apparently is so only through coincidence, for its original habitat is seemingly dry rocky hills. But the other

[6] This principle, which from its discoverers we may call the KIHLMAN-GOEBEL principle, seems to me deserving of much more recognition than our students are inclined to give it. At least it calls for careful experimental investigation.

two, the waxberry and the Hudsonia, are characteristic of just this situation, in and to which they have apparently been adaptively developed. Towards the inner dune beaches another low shrub comes in on the slopes, though dwarfed and not abundant, the common blueberry, *Vaccinium pennsylvanicum;* it is evidently not here at home, but its somewhat xerophytic habit permits it to exist. As these various plants grow older and extend their patches, they run together more or less, sometimes two, sometimes three, and even all four. Later others are added to them, initiating the juniper mats and the woods carpet, later to be considered.

The contrast between the vegetation of the outer and the sheltered slopes of the dune beaches comes out with striking clearness a few hundred yards north of Eel Brook, where it happens the entire plain is very narrow, and slopes in both directions from a central higher crest. Outside of this can be seen only the beach grass and its accompanying forms as listed above, while inside the various xerophytic shrubs show to great perfection.

THE SWALES.

Between the open grass plain and the woods occurs a transition zone marked not only by an intermediate vegetation but also by distinctive physical features as well. First of all it is characterized by the presence of several great turf-carpeted and tree-bordered swales, morphologically hollows between the dune beaches which here spread much farther apart than usual. They are well shown in *figs. 8, 10, 11.* They are best developed in the widest part of the plain, hardly occurring towards its southern or northern ends, and outside of them runs a line of higher dune beaches, which indeed can be traced through most or all the length of the plain (*fig. 2*). The swales are narrow southward, but broaden northward, deepening as they go, until in some cases they dip beneath the water-table (thus exhibiting pools), after which they rapidly narrow and rise to disappear northward. Again, the trees of this zone, occurring always along the slopes of the dune beaches, do not exhibit a transition of size and age to those of the sandy woods, but are always so much smaller and younger as to be sharply marked off from them, the case shown in *fig. 10* being very exceptional, and that of *fig. 8*

more typical. Again, the transition from the broad swales to the beaches of the sandy woods is most abrupt, for the latter are regular, narrow, close together with scarcely any hollows between, and also exhibit a curious barrenness on their summits in marked contrast to the better-clothed summits farther out (compare *figs. 8* and *13*). Unfortunately the full importance of these features did not strike me in time for a study of them on the ground, but such data as I possess in notes and maps lead me to believe that the swales are much newer in origin than the beaches immediately inside them, and that they mark the transition from an older series of beaches which formed part of the original Grande Plaine extending far to

FIG. 8.—Typical transition zone, looking north; showing a swale on the right, with its sharp line of transition to the woods; the trees are all white spruce.

the north of the present island, and a newer series formed by the rolling of the plain down the coast, as described earlier in this paper. All the facts I possess both as to geography and vegetation are consistent with this view.[7]

Aside from the question of age, the swale zone differs physically from the grass plain by its greater shelter from the west winds, its lower level and greater nearness to the water-table, a probable increase of mineral nutrients derived from decaying driftwood and diffusion from the upland, and some slight accumulation of humus.

[7] And it is sustained by the tradition of the residents who say that the plain has been built out from the edge of the woods almost within the memory of men still living. I have discussed the subject more fully in Bull. Nat. Hist. Soc. N. B. No. 24:456. 1906.

The vegetation consists broadly of a higher development of the vegetation of the inner grass plain—the scanty turf of the hollows becoming the broad expanse of meadow turf of the swales, and the juniper mats extending greatly with the addition of many young white spruces. So distinct are the turf of the swales and the juniper mats, with their trees, from one another, that there result glades and vistas of park-like and charming aspect, as shown especially well in *fig. 8*.

First in importance are the juniper mats, for they inaugurate the woods. These mats, composed either of large radiating patches of this plant, or else variously united and combined with patches of waxberry, Hudsonia, and blueberry, extend greatly in diameter, covering the crests as well as the slopes of the dune beaches, and thus form a woody net in the shelter of which several other forms, mostly markedly dwarfed, gain foothold. A typical example is shown in *fig. 9*. Some of the plants of the grass plain persist, especially the beach grass, pearly everlasting, and yarrow. The new forms which appear are, first of all, the common crowberry, *Empetrum nigrum*, and the rock cranberry, *Vaccinium Vitis-Idaea minor*, followed closely by the three-toothed cinquefoil, *Potentilla tridentata*, all of them plants characteristic of dry upland rocky situations. Less frequent are the little gentian, *Gentiana Amarella acuta*, and the large cranberry, *Vaccinium macrocarpon*, plants belonging to moist places. And when the mats are especially well developed there come in, as shown in *fig. 9*, the reindeer lichen, *Cladonia rangifera*, and a brown moss which I take to be the *Aulacomnium palustre* (so much more highly developed in the woods), another curious mixture of xerophytic and hydrophytic forms. We have therefore upon these juniper mats a very heterogeneous assemblage of forms drawn from diverse natural habitats all the way from rocky hills to bogs. They do not exist here, therefore, in virtue of adaptation to this position, but plainly represent those forms of the flora of this region whose adaptations happen to fit these conditions, or whose range of physiological toleration happens to be great enough to permit endurance of the conditions here. Of these matters we shall know more in the future, but their mention helps to emphasize how large an element of accident or incident

there is in adaptation, and how likely it is that adaptation will ultimately prove to be a matter of the loose and large rather than of the exact and minute.

Finally, it is in this same situation, upon the upper slopes of the dune beaches, and usually, but not always, on the juniper mats, that the characteristic trees of the zone, the white spruce, *Picea alba*, develop. Standing in open formation, they do not interfere with one another's growth, and in consequence become,

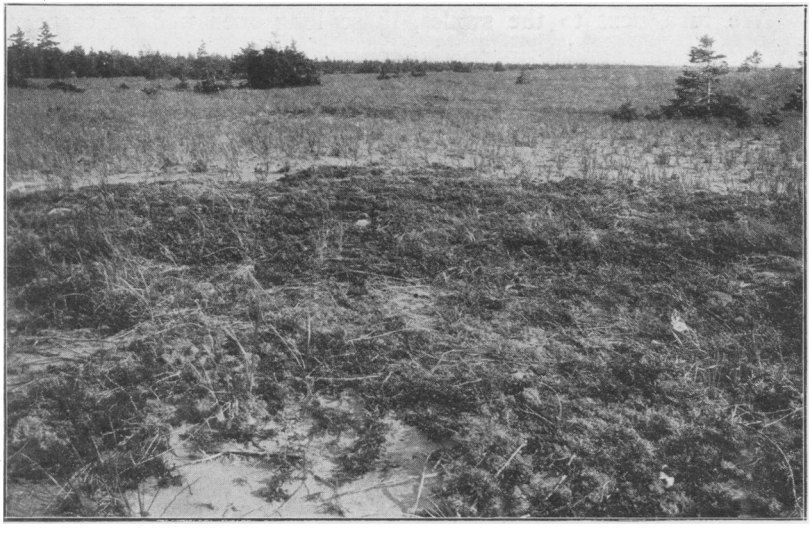

FIG. 9.—Typical large juniper mat on a slope and crest of a dune beach, with a number of associated plants noted in the text; looking south.

except for wind effects, symmetrical in outline and clothed to the ground. They occupy that situation no doubt for the same reason that the shrubs do, as a compromise between the greater wetness of the hollows and the greater dryness of the beach summits. This habit of growing thus upon the slopes, and not on summits or hollows, has a most important effect upon the physiognomy of the vegetation in this zone; for to it is due the openness of the swales, with their regular borders of trees, and as well the openness of the beach summits in the sandy woods later to be noticed. Toward the sea the spruces are small and dense, and often show, as in *fig. 11*,

pronounced wind effects. In places many seedling trees may be found, though the distribution of these is curiously irregular. In one place only did I find any other tree, and that was a single specimen of the prince's pine, *Pinus Banksiana.*

If it be asked why the white spruce is the first tree to develop on these plains instead of some other of those growing on the upland near by, I can only say that an answer must wait until we know something about the physiology of the white spruce and of other trees of the vicinity.

We turn next to the swales, those long open hollows carpeted by a close turf, and bordered by spruces. The general appearance

FIG. 10.—Highly developed swale, looking south; on the left is the edge of the sandy woods with old trees, and on the right a line of much younger trees, here much larger than usual.

of the turf is well shown on the right in *fig. 8*, and extremely well in *fig. 10*, which shows perhaps the best-developed of all the swales. The turf is a good deal modified in vegetation by the grazing of cattle and horses, yet its general characters show plainly enough. Originating in the outer hollows with the strawberry, as already noted, the real turf begins with the red fescue grass, *Festuca rubra* (*F. ovina rubra*), which soon drives out the strawberry. To this, as it becomes compact in the inner hollows, other grasses are rapidly added, especially the June grass, *Poa pratensis*, and then the brown top, *Agrostis alba*. After these comes a rush, *Juncus Vaseyi*, and the little sedge, *Carex Oederi*. Very likely, also, there are other

grasses which, owing to my imperfect knowledge of those groups, I overlooked. On and among these plants occur others, among which I have collected the following: the eyebright, *Euphrasia americana* (*E. officinalis*); the bugle weed, *Lycopus uniflorus* (*L. virginianus*); a tiny everlasting, *Antennaria neodioica;* a pearlwort, *Sagina procumbens;* the plantain, *Plantago major;* the two common cinquefoils, *Potentilla norvegica* and *Anserina;* the fall dandelion, *Leontodon autumnale;* and the white clover, *Trifolium repens.* These forms, in common with the grasses, are all greatly dwarfed

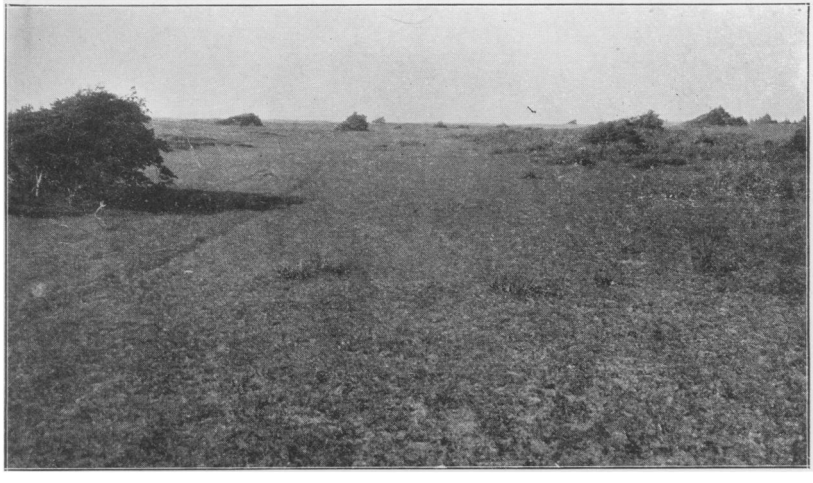

FIG. 11.—An outer swale, looking north; in the center clumps of blue flag; on the slope on the left white spruce and waxberry; on the right is a low depression with a thicket of poplar (the white spruce among it being on a local elevation).

and derived from diverse habitats, and are evidently a collection of heterogeneous stragglers from the neighborhood, held together by no stronger bond than ability to eke out existence in this inhospitable position. The majority belong to somewhat moist places, and they find an ample supply of water; for the water-table even in the driest summer is within a foot of the surface, and of the sweetest water. Evidently it is not dryness which stunts the forms, but most likely, as I believe, paucity of mineral nutrients. The turf represents the first closed formation we have met with, and

competition may therefore determine some of its minor features, but to these I gave no attention.

The turf reaches its climax in the open swales like those shown by *fig. 10*. In the woods it disappears, as will be noted under the next section; but towards the lower levels, especially towards the pools of standing water, it gives way gradually, by definite steps, to an assemblage of true swamp plants. The very first of these to appear in the lower places in the swales is always the common blue flag, *Iris versicolor*, and characteristic scattered clumps of this plant may be seen in the foreground in *fig. 11*, in the distance

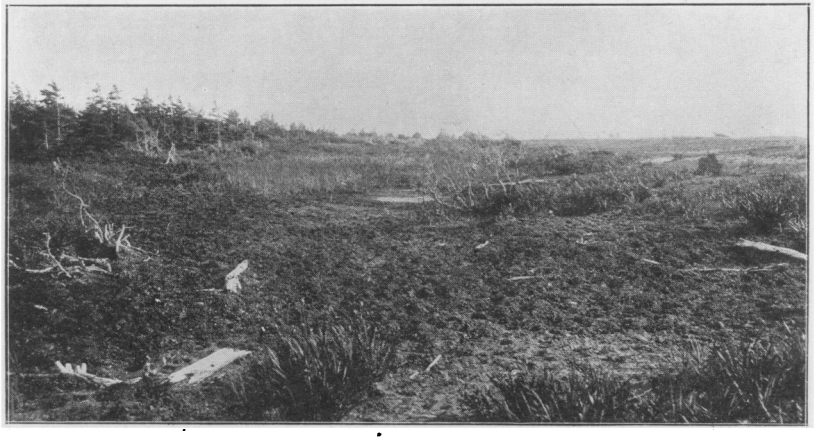

FIG. 12.—Marshy swale, looking south; in the center a permanent pool with margin trodden by cattle; behind it are cat-tails and rushes, and back of them a thicket of poplar; on both right and left is sweet gale, and in the foreground is the blue flag.

on the swale in *fig. 8*, and on the left margin of the swale in *fig. 10*. Next follows always the sweet gale, *Myrica Gale*, and after that low bushes of the balsam poplar, *Populus balsamifera*, a plant which forms very dense thickets and grows larger as the situation is more sheltered. Finally the pools of standing water are reached, and on their margin occur cat-tails, rushes, and mare's tail, *Hippuris vulgaris*, with some other forms which I have not attempted especially to study. The plants may be variously combined according to local circumstances, but a very typical arrangement is shown in *fig. 12*. It is plain that we are dealing here simply with an ordinary

swamp, offering nothing peculiar unless it be the small size of some of the plants, notably the poplar. But these places develop yet farther in time, and there come in after the poplar three willows: *Salix balsamifera*, *S. lucida*, and *S. candida*, forming very dense thickets, and apparently under congenial conditions. Finally comes in the alder, which appears to be mostly a form of the green alder, *Alnus mollis*, giving us the culmination of the swale thickets.

THE SANDY WOODS.

Inside the swale zone, through almost the whole length of the plain, extends a narrow zone, only some four or five dune beaches

FIG. 13.—Typical sandy woods, just inside the swales, looking north; in the center a dune beach, bearing scanty beach grass and reindeer lichen, while on the slopes are small juniper mats with white spruces.

wide, of remarkable sandy woods, whose characters are well shown by *fig. 13*. Their most striking feature is perhaps the relative bareness of the tops of the beaches, which remain far more clear of vegetation than do most of the beaches outside of them; and this bareness, in conjunction with the presence of trees on the slopes and in the hollows, gives rise to curious vistas as shown by the photograph. The bareness must have some physical basis, but I was not able to discover it. These dune beaches, further, are very narrow, low, and regular, with hardly any true hollows between, so that the turf

from the swales is very scanty, almost wanting, in this zone. Further, the trees, all of them white spruces, are much older than those of the swale zone, the transition being commonly of the most marked abruptness. All of these features tend to emphasize the conclusion earlier given, that there is an abrupt physical difference between the beaches of these woods and those outside, a difference which, I feel sure, is one of age. The position of the zone would indicate that it possesses more favorable physical conditions as to water, mineral supply, and shelter than the zone outside, with which the large size of the trees is in agreement. But the bigness of the trees makes the barrenness of the beaches all the harder to explain. In their vegetation the sandy woods exhibit three divisions: the sparse, scattered beach grass and reindeer lichen (*fig. 13*) on the beach crests already mentioned; a few and small patches of turf which can hardly obtain a foothold where the hollows are so small; and the juniper mats in the slopes and hollows with their well-grown white spruces. The mats, however, are no longer entirely creeping, for the junipers send up numerous erect shoots. With them persist several of the plants from the transition zone, especially the rock cranberry, the three-toothed cinquefoil, the pearly everlasting, and a few others. But in addition new forms come in, especially and characteristically the bearberry, *Arctostaphylos Uva-ursi*, a rocky-hill plant, here creeping radiately over the sand, apparently under congenial conditions. Beneath the shelter of the trees appear some plants of the woods carpet which we may best consider under the next section. The trees themselves are of moderate size, rarely if ever over 20 feet in height.

A fact of interest about the juniper mats, applying also to a less degree to the forest mat which succeeds it in the closed woods, is its very slight hold upon existence on the sand, for where teams cross and disturb it, the entire mat dies and soon disappears. Such instability shows forcibly how hard are the conditions of life in this situation, and how narrow the margin between success and failure.

THE CLOSED WOODS.

The climax of the sand-plain vegetation is reached in the dense though dwarfed mixed woods extending between the sandy woods and the upland. A typical view of the closed woods is shown by *fig. 14*.

Physically the situation is much more protected than the zones outside of it, and, lying at a still lower level, it has a moister soil. The soil, however, is still of sand, though it contains some humus from the decaying vegetation and must derive some mineral matter by diffusion and drainage from the upland. Very likely also the sand is shallower here than farther out (*fig. 2*), and hence some influence of the minerals of the underlying soil may be felt, while in places an appreciable enriching of the soil must result from the decay of

FIG. 14.—Typical closed woods, chiefly of white spruce, but with some deciduous trees in the background; the closed forest carpet shows in the glade of the left foreground.

the bodies of the walrus, formerly slain here in great numbers, as manifest by their semi-fossil bones.[8] These additional sources of mineral nutrients, however, by no means furnish a supply sufficient for the proper growth of the woods, for in every feature they exhibit marked depauperation as compared with the same species on the neighboring upland.

In relation to the preceding zone, the closed woods consist essen-

[8] Described more fully in a note in Bull. Nat. Hist. Soc. N. B. No. 24:462. 1906.

tially of a greater development of the juniper mats, which unite to form a complete unbroken carpet, together with a greater development, both in number and size, of the white spruce trees, to which are added some deciduous trees and shrubs. And where the hollows dip lower than usual, and towards the upland in places, this forest merges to alder and cedar swamp.

We consider first the woods carpet. Morphologically it is a direct development of the juniper mats of the outer zones, though but little juniper, aside from occasional erect shoots, is left. With it persist some of its earlier associates, the rock cranberry, three-leaved cinquefoil, some grasses, the bearberry, and the reindeer lichen, varying in their respective development according to situation. To these are now added dwarf plants of the bunchberry, *Cornus canadensis*, the twin flower, *Linnaea borealis americana*, *Pyrola chlorantha*, the pipsissewa, *Chimaphila umbellata*, and an abundant brown moss, which has been identified for me by Mr. A. J. GROUT as *Aulacomnium palustre*, a typical swamp moss. Upon this carpet develop a few larger forms, especially the abundant wild sarsaparilla, *Aralia nudicaulis*, the gooseberry, *Ribes oxyacanthoides*, the dwarf raspberry, *Rubus triflorus*, with others less conspicuous.

We consider next the trees of these woods. First in importance and size, far surpassing all others in both respects, is the white spruce. It attains a height of perhaps 7.5^{m}, a diameter near the ground of perhaps 45^{cm}, and it exhibits over 100 annual rings, though perhaps some may be much older than those I counted, which were cut by the residents for wood. The next to appear is the balsam fir, *Abies balsamea*, becoming somewhat abundant and characterized by a spruce-like arrangement of its leaves all around the stems. Then follow the red maple, *Acer rubrum*, the aspen, *Populus tremuloides*, the paper birch, *Betula alba papyrifera* (in very small trees however), and the mountain ash, *Pyrus americana;* while the common undershrubs are the red dogwood, *Cornus stolonifera*, and the black alder, *Ilex verticillata*. There are probably some others, but these I believe are all that are notable.

In especially low places, such as in certain hollows, and at the contact of plain and upland, the conditions verge towards those of

a swamp, and swamp plants appear—the iris, the sweet gale, some mints, species of Galium, and the dewberry; while the spruce gives way to the white cedar, *Thuja occidentalis*, and the alder becomes abundant, forming a dense jungle. But this is of less interest than the vegetation of the outer zones, and hence I gave it little study.

Thus it appears that these woods present no features, size of the plants alone excepted, markedly different from those of woods preponderatingly coniferous in the neighboring upland, and they are evidently tending towards the typical woods of this region—the mixed coniferous-deciduous forest.

We have thus another illustration of that principle so important in physiognomic ecology, that vegetation, no matter under what immediate physical conditions it may be, is always tending towards a climax type, determined primarily by climate.

CONCLUSION.

In this paper I have tried to state the facts about the vegetation of a somewhat remarkable place, adding thereto some ecological comment whose chief value is to illustrate our ignorance of that subject. As I understand it, such descriptions as this aims to be may have three values. First, they can present to all who have interest in such matters a series of pictures, as vivid and realistic as possible, of the vegetation of special places, and they are the more valuable according as they are the more clearly and attractively written and the more aptly illustrated. Second, they should help to supply information, badly needed by all of our manuals, about the natural habitats of the common or important species of plants. Third, they can form storehouses of facts about vegetation upon which the future student can draw as the advance of physiological ecology gradually makes possible an understanding of the principles underlying physiognomic ecology. Such descriptive work can be done to profit by the student whose work is perforce confined to his summer vacations, if he but bring to it time and care enough; but he should be content to describe well and to leave interpretation to the field physiologist yet to come. Speculation cannot of itself advance knowledge, and it can bring a subject into disrepute. It is only, I believe, through field physiology, the study

in field laboratories of fundamental plant-dynamics, that ecological knowledge can really be advanced. And the dynamical problems, as I see them, fall under these heads, in the order of importance: (*a*) physiological life-histories of species, (*b*) physics and chemistry of the soil, (*c*) nature of plant-competition, (*d*) a better correlation of meteorological data with physiological phenomena.

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